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Notes and Comments

Evolution of the Hominid Hand and Tool Making Behavior

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Marzke (1997) has identified eight anatomical traits of the human hand that together facilitate precision pinching and precision handling. Her study sheds light on the anatomical traits necessary for the advent of tool-making and the efficiency of tool-using behavior in human evolution. Marzke's study goes far beyond inferences from fossil hand bones and simplistic discriminations between humans and living hominoids and as such will be a valuable foundation for future research on this problem.

Marzke's approach, while clearly more empirical and comprehensive than preceding ones, is still founded on qualitative data derived from anatomically modern humans. The complete package of traits that Marzke has evaluated may reflect sequential acquisition of manipulative characters rather than the minimum combination necessary to initiate efficient manufacture and use of tools. The evolution of bidpedality poses a similar problem for comparative anatomy. The many traits of the modern human skeleton that relate to upright posture and efficient striding bipedalism evolved sequentially; to score a modern human skeleton for a combination of critical traits may capture key anatomical "enablers," but such an approach fails to account for the evolutionary unfolding of preconditions and exaptations that we believe are the key to understanding innovative tool-making and tool-using behaviors.

We believe that the deepest understanding of a biobehavioral phenomenon such as precision manipulation comes from an appreciation of the hand as the endpoint of the upper limb, both developmentally and evolutionarily; as such, the hand's ability to precisely manipulate objects depends largely on its anatomical configuration at the time that the hominid upper limb no longer served a weight support and locomotor function. Gebo (1996) and Hunt (1996) recently have proposed detailed and reasonable, yet conflicting, hypotheses of the origins of bipedalism. For the sake of this argument, let us assume that one of them is correct. Because they both place different selective pressures on hand and wrist morphology prior to erect posture and bipedal locomotion, the choice of which model is correct changes the preadaptive starting point for the evolution of precision grip morphology. Gebo's (1996) model requires a protohominid wrist configured for terrestrial quadrupedal weight support. This would include limitations on carpal and metacarpal joint mobility imposed by the joint stability necessary to support compression forces of body weight during locomotion. By contrast, Hunt's (1996) feeding posture model requires a protohominid hand morphology adapted only to tensile weight support, complete with the mobility necessary for an arboreal climbing and suspensory lifestyle. The "correct" model in this simulation disposes the hominid hand to very different preconditions for precision manipulation, and thus the traits of such a complex are subject to very different evolutionary polarities.

Although dealing with a different aspect of human evolution, Churchill (1996) has illustrated the importance of distinguishing between particulate and integrative evolutionary pathways. The former assumes that the comparative anatomy of isolated regions

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or individual trait complexes reflects biological and behavioral adaptations, while the latter assumes that anatomical changes in specific parts of the body result from shifts in overall body form. We posit that the hand morphology implicated in the evolution of precision manipulation in humans conforms with Churchill's (1996:559) observation of "a high degree of tolerance for particulate evolution in the context of an integrated upper body plan." Marzke's (1997) eight anatomical traits of tool manufacture and use include some that probably were part of the integration of the upper limb for locomotion just prior to the advent of bipedality, some that directly enable the controlled flaking of stone, and some that evolved over time in a particulate response to the benefits of efficient precision gripping.

We promote the study of precision manipulation in a context broader than the question of whether or not a particular hominid species could have made tools or via a narrow focus on the biomechanics of tool use. As a target goal for studies of the evolution of manipulation these approaches inflate the significance of threshold traits and deflate the significance of preadaptations, respectively. Marzke's (1997) study has advanced the comparative anatomy of manipulation to a level that now requires interpretive rooting in integrative rather than particulate evolution. The evolution of precision manipulation is the story of bipedalism, relaxed selection on upper limb joint stability, and the exploitation of progressive efficiency in the application of a preadapted biobehavioral grasping complex.

LITERATURE CITED

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Reply

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Hartwig and Doneski imply an evolutionary scenario in which an ancestral hand, specialized for quadrupedal locomotion but preadapted for precision manipulation, does not begin precisely manipulating objects until it is released from locomotor duties by the origin of bipedality. At the time of release, precision manipulation by the earliest bipedal hominids exploits some of the locomotor features compatible with precision manipulation of tools, which are later supplemented by additional features favorable to tool manipulation.

They contrast this scenario with their own revision of Marzke (1997), in which her so-called "complete package of traits, . . . the minimum combination necessary to initiate efficient manufacture and use of tools," is imposed at one point in time upon an ancestral hand that has been freed from locomotion but lacks facility for precision manipulation.

Contrary to statements by Hartwig and Doneski, the eight traits to which they refer were not presented in Marzke (1997) as having appeared together, nor were they described as a complete package or as a minimum combination necessary to initiate efficient manufacture and use of tools. In fact, 1) their possible sequential order of appearance in the record was traced in the section of the paper on fossil evidence for stages in the evolution of precision grip capabilities and tool behaviors, and 2) the combination of traits was recommended for

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